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1 Running head: Ungulates and N availability in space

2

3 Title: Broadening the ecological context of ungulate-ecosystem interactions: the importance of
4 space, seasonality, and nitrogen

5

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10 ABSTRACT

11 Spatial heterogeneity of soil resources, particularly nitrogen availability, affects herbaceous-layer
 12 cover and diversity in temperate forest ecosystems. Current hypotheses predict that ungulate
 13 herbivores influence nitrogen availability at the stand scale, but how ungulates affect nitrogen
 14 availability at finer spatial scales that are relevant to the herb-layer is less understood. We tested
 15 the hypothesis that ungulate exclusion reduces the spatial complexity of nitrogen availability at
 16 neighborhood scales (1-26m) apart from mean stand scale effects. This outcome was expected
 17 due to a lack of ungulate nitrogenous waste deposition within exclosures and seasonally variable
 18 ungulate habitat use. To test this hypothesis we examined spatial patterning of ammonium and
 19 nitrate availability, herb-layer cover and diversity, and under-canopy solar radiation using
 20 geostatistical models. Our study sites included 6 stands of eastern hemlock (*Tsuga canadensis*)
 21 forest: 3 where white-tailed deer (*Odocoileus virginianus*) were excluded and 3 that were
 22 accessible to deer. Where deer were present patch sizes of ammonium availability, cover, and
 23 diversity were smaller compared to deer exclosures whereas mean site level effects were not
 24 significant. Within deer exclosures cover and solar radiation were more similar in patch size than
 25 were cover and nitrogen availability. Our results suggest that browsing ungulates affect spatial
 26 patterns of herb-layer cover and diversity through the excretion of nitrogenous wastes in small,
 27 discrete patches. Ungulate-excreted nitrogen deposition and herbivory was concentrated in the
 28 dormant season, allowing herb-layer plants a greater opportunity to benefit from nitrogen
 29 additions. Therefore, the impact of ungulates on nitrogen cycling in forest ecosystems varies
 30 with spatial scale and the seasonal timing of ungulate impacts. In this way, ungulates may
 31 function as a seasonally-dependent link between fine scale and landscape level ecological
 32 processes.

33 *Key words: context dependence, diversity, eastern hemlock, habitat use, herbaceous layer,*
 34 *heterogeneity, nitrogen, Odocoileus virginianus, spatial patterning, temperate forest, Tsuga*
 35 *canadensis, white-tailed deer*

36

37 INTRODUCTION

38 Determining what controls spatial and temporal patterns of nitrogen availability has
 39 important implications for understanding and maintaining key ecosystem functions (Gilliam
 40 2006). Nitrogen is a limiting resource to primary production in many terrestrial ecosystems
 41 (Vitousek and Howarth 1991), and processes that influence spatial patterns in nitrogen
 42 availability influence plant biomass, competitive relationships, and thereby biodiversity
 43 (Vitousek et al. 1997, Gilliam 2006). Nitrogen availability is often homogenized by current
 44 human activities, especially via atmospheric deposition, which emphasizes the need to
 45 understand the mechanisms and context dependence (*sensu* Schmitz 2010) of processes that
 46 affect nitrogen heterogeneity. Such an understanding is important to address the homogenizing
 47 effects of human activities and develop a predictive understanding of ecosystem function.

48 The seasonal redistribution of nitrogen by animals such as ungulate herbivores is an
 49 important mechanism that tends to increase the spatial heterogeneity of nitrogen in terrestrial
 50 ecosystems (Steinauer and Collins 1995, Augustine and Frank 2001). Ungulate herbivores affect
 51 nitrogen availability through direct and indirect mechanisms. Direct effects occur by ungulates
 52 ingesting nitrogen from across the landscape and concentrating it into hotspots of excreta
 53 (Steinauer and Collins 1995, Augustine and Frank 2001, Peek and Forseth 2003) and carcasses
 54 (Bump et al. 2009b). Seasonal or diurnal habitat use patterns can facilitate a net transport of
 55 nitrogen across habitat boundaries (Seagle 2003, Abbas et al. 2012). Indirect effects occur due to

56 preferential browsing of more palatable plant species, resulting in a plant community transition
 57 toward less nutritious species that produce lower quality leaf litter for decomposers. As a result,
 58 nitrogen availability to soil biota and associated processes declines (Pastor et al. 1993, Bardgett
 59 and Wardle 2003, Bressette et al. 2012).

60 Although available evidence indicates that ungulates generally decelerate nitrogen
 61 cycling rates in forest ecosystems via indirect effects (Ritchie et al. 1998, reviewed in Pastor et
 62 al. 2006), few studies have addressed the importance of spatial heterogeneity at fine spatial
 63 scales of 1-20 m, which are influential in herbaceous-layer community dynamics (Frelich 2002,
 64 Gilliam 2007). In grasslands, ungulate excreta can increase heterogeneity of nitrogen availability
 65 at such fine scales (Steinauer and Collins 1995, Augustine and Frank 2001, Peek and Forseth
 66 2003). Ungulate carcasses can generate nutrient hotspots for vegetation growth in grasslands
 67 (Towne 2000) and forest understories (Bump et al. 2009b). Modeling of ungulate habitat use
 68 patterns and nitrogen excretion rates suggests that impacts are expected to be heterogeneous at
 69 the landscape scale (Seagle 2003, Abbas et al. 2012). Ungulate effects on landscape- and local-
 70 scale nitrogen availability may link coarse- and fine-scale processes, as does ungulate herbivory
 71 (Hurley et al. 2012).

72 We tested the hypothesis that stands with ungulate access would have more complex fine
 73 scale spatial patterns of nitrogen availability and detectable nitrogen hotspots compared to
 74 exclosures, but exhibit no difference in mean nitrogen availability at the stand scale. If true, we
 75 also expected herb-layer cover and diversity to exhibit differences in spatial patterns at fine
 76 scales, but not necessarily mean differences at the stand scale. We expected greater complexity
 77 in spatial patterns of nitrogen availability due to deposition of ungulate excreta in discrete
 78 patches (Steinauer and Collins 1995, Augustine and Frank 2001). Increased nitrogen availability

79 would increase plant growth rates (Peek and Forseth 2003) given that primary production in
 80 temperate forests is often nitrogen-limited (Vitousek and Howarth 1991) and temperate forest
 81 plants often possess adaptations to rapidly capitalize on ephemeral nitrogen pulses (Farley and
 82 Fitter 1999). We did not expect considerable consumptive effects because the seasonal timing of
 83 nitrogen inputs and herbivory are decoupled in our study system (Jensen et al. 2011, Witt et al.
 84 2012). Ungulate use, and therefore nitrogen deposition and herbivory, occur mainly during the
 85 dormant season, allowing herbaceous plants increased nitrogen availability and reduced
 86 herbivory risk during the growing season. We tested this hypothesis using 3 large ungulate
 87 exclosures (up to 30 ha) and 3 nearby unexclosed sites located in winter ungulate habitat. Our
 88 within-site sampling design captured spatial variance at a scale of 1-26 m, which is relevant to
 89 herb-layer community interactions (Frelich 2002, Gilliam 2007). These analyses address the
 90 fundamental questions: at what spatial scales do ungulates affect nitrogen availability and what
 91 are the implications for herbaceous-layer vegetation?

92
 93 METHODS

94 *Study sites*

95 Our study occurred in six eastern hemlock (*Tsuga canadensis*)-dominated stands in the
 96 western Upper Peninsula of Michigan (Appendix A, Fig. A1). Three stands (Boneyard, Spree,
 97 and Walton Creek) were entirely enclosed by a 2m tall fence that excluded white-tailed deer
 98 (*Odocoileus virginianus*) while allowing access to smaller animals. Three other stands (Ford
 99 Forestry Center, Silver River, and Sylvania) were accessible to deer. Deer exclosures were
 100 constructed in 2003 (Walton Creek) and 2007 (Boneyard and Spree). Deer access sites were
 101 selected from a set of 39 remnant hemlock stands in the western Upper Peninsula where winter

102 deer use has been monitored since 2006 (see Appendix B, B.1 and Witt and Webster 2010 for
 103 details). The deer access site selection criteria in the current study included high deer use during
 104 2006-2010, intermediate size (10-30 ha), and similar soil type and forest structure to the
 105 previously-constructed exclosures (see Appendix A, Table A1 for site information). Prior to the
 106 study year of 2011, the selected access sites experienced winter deer use well above the 39-site
 107 average. Growing season deer use was considerably less than winter deer use, and growing
 108 season deer herbivory was also less than expected based on winter deer use (Witt et al. 2010,
 109 Jensen et al. 2011). The deer exclosures used in our study, at 4 ha and 30 ha area, were unusually
 110 large for temperate forest regions.

111

112 *Sampling design*

113 A cyclical sampling network was used to efficiently measure spatial patterning across a
 114 range of scales from single tree (1-10m) to neighborhood (10-20m; Frelich 2002). At each site, 1
 115 x 1m quadrants were placed in a repeating cycle of 0, 1, 3, and 9m every 13m along two
 116 intersecting 52m transects. Transects intersected at the midpoint at a 60° angle (see Appendix B,
 117 Fig. B1 for a diagram). This sampling design maximized spatial information gained from as few
 118 sample points as possible (Clinger and Van Ness 1976, Scheller and Mladenoff 2002). Sample
 119 size was 33 quadrants at each site, or 99 quadrants per treatment, for a grand total of 198
 120 quadrants.

121

122 *Field data collection*

123 Herb-layer vegetation was sampled by a visual survey of cover by species in each
 124 quadrant. We chose cover as a surrogate for biomass to reduce our impact on the forest, and

125 because it is a reliable indicator of biomass (Hermy 1988). The same observer conducted all
 126 surveys to maintain consistency. Herb-layer vegetation was defined as all plants <1.0m in height.
 127 Individual plants were grouped by species, with the exception of the Division Bryophyta, into the
 128 following cover classes: 0, 1, 5, 10, 25, 50, 75, 90, 95, and 99% (McCune and Grace 2002).
 129 Early summer herb-layer species were sampled on 6-11 June 2011, whereas late summer species
 130 were sampled on 25, 27, or 29 July. A nonmetric multidimensional scaling ordination procedure
 131 conducted in PC-ORD 5 (McCune and Mefford 2006) did not reveal a stable structure for herb-
 132 layer cover data (final stress = 37.7; instability = 0.046; 500 iterations).

133 The abundance of woody vegetation was measured in three size classes: seedlings
 134 (<0.25m height), saplings (0.25-3.00m height, <10.0cm diameter at breast height
 135 (DBH=1.37m)), and trees (≥ 10.0 cm DBH). The number of seedlings was counted by species in
 136 each quadrant. Saplings were counted by species and height was recorded. Trees were quantified
 137 by 5 variable-radius plots (basal area factor = $2.3 \text{ m}^2 \text{ ha}^{-1}$) at each site. The center of a variable-
 138 radius plot was located at each transect terminus as well as the intersection of transects. Our
 139 sampling area for saplings and overstory trees was small and intended for descriptive purposes
 140 only.

141 Nitrogen ion availability was assessed by burying ion-exchange resin beads *in situ*,
 142 extracting the adsorbed ions in the laboratory, and colorimetrically measuring ammonium and
 143 nitrate concentrations of the extracts (described in Appendix B, B.2). Four resin bags were
 144 buried at 5-10cm depth in each quadrant for 91 days (7-12 March through 6-11 June 2011). We
 145 chose this time period to capture nitrogen availability from spring snowmelt through
 146 establishment of the early summer understory flora.

147 The availability of light to herb-layer vegetation was estimated from digital
 148 hemispherical photographs of the canopy. Hemispherical photographs were taken from 1m
 149 height during the 6-11 June sampling period. Direct and diffuse under-canopy radiation (mean
 150 photosynthetically active flux density, $\text{mol m}^{-2} \text{day}^{-1}$) was computed using the computer software
 151 WinSCANOPY (WinSCANOPY 2005) and a growing season length of 1 May through 30
 152 September.

153 The location of deer excreta along transects was measured by visually searching for fecal
 154 pellet groups. A pellet group was counted if it was located within 1.5m of the transect center, so
 155 that 321 m^2 was searched for pellet groups at each deer access site. Quadrants were visually
 156 inspected for earthworm middens, but none were observed.

157
 158 *Site level comparisons*

159 Site level means of variables were computed as the mean of quadrant-level observations.
 160 We determined total percent cover as the sum of cover class midpoints of all species present in a
 161 quadrant. Seedling density was computed as the total number of seedlings m^{-2} . Sapling density
 162 was computed in the same manner. We determined species richness (S), Shannon's diversity
 163 index (H') and evenness (E) for each quadrant.

164 We compared stand level means in nitrogen availability, under-canopy radiation, and
 165 vegetation attributes between deer access and exclosure sites. Monte Carlo randomization tests
 166 on absolute mean differences (Gotelli and Ellison 2004) were used because most variables did
 167 not approximate a normal distribution. The null distribution was generated with 1000
 168 permutations. Stand level means were considered to be statistically significantly different if $p <$
 169 0.05. Monte Carlo randomization tests were also performed on the 90th percentiles of

170 ammonium, nitrate, and total nitrogen ion (sum of ammonium and nitrate by quadrant) to test the
 171 hypothesis of greater nitrogen hotspots in deer access sites. We chose the 90th percentile to test
 172 this hypothesis because it is more sensitive than the mean to extreme values.

173

174 *Spatial analyses*

175 Spatial patterning in nitrogen availability, under-canopy radiation, herb-layer cover, and
 176 diversity were compared using semivariance analysis (Goovaerts 1998). Semivariance ($\gamma(h)$)
 177 measures the spatial variance between sample points at variable separation distances (h).
 178 Semivariance was standardized by dividing by the sample variance s^2 so that all semivariograms
 179 would be on the same scale for direct comparison. Also, a standardized semivariance less than 1
 180 (semivariance < sample variance) indicates spatial dependence between sample points at a given
 181 separation distance. Standardized semivariance was computed for each h up to half the transect
 182 length (1-26m) using the R statistical environment (R 2012) and the packages RGDAL (Keitt et
 183 al. 2012) and GSTAT (Pebesma et al. 2004). We used the package GGPlot2 (Wickham 2009)
 184 to generate empirical semivariograms by plotting observed $\gamma(h)$ by h . All variables except
 185 diversity required a Box-Cox transformation ($n = 198$ observations) to achieve normality prior to
 186 semivariance analysis.

187 We modeled spatial patterning in each variable by fitting 5 candidate models to each
 188 empirical semivariogram and selecting the most parsimonious model through an information-
 189 theoretic approach. We chose 5 models that are often useful for describing spatial patterning of
 190 variance: white noise (no systematic change in variance with increasing separation distance),
 191 linear (algebraic change in variance), spherical, exponential, and Gaussian (rapid change in
 192 variance at small separation distances that decreases at larger distances) (see Appendix B, Table

193 B1 for model equations). The white noise model is a single-parameter model that represents
 194 random variation in variance with increasing h . The linear model contains slope (m) and y-
 195 intercept (γ_0) parameters and indicates a linear change in spatial dependence. The spherical,
 196 exponential, and Gaussian models each contain three parameters which represent the range of
 197 spatial dependence (a), the partial sill (C) which represents spatial variance explained by the
 198 model, and the nugget (ϵ) which represents spatial variance at distances shorter than the step size
 199 as well as sampling error. For the spherical model the partial sill C is the limit of $\gamma(h)$ as $h \rightarrow a$.
 200 The exponential and Gaussian models also reach C asymptotically, but the practical range a must
 201 be estimated from the range parameter b . The practical range is reached when $\gamma(h) = 0.95(C)$,
 202 which can be computed by $a = 3b$ for the exponential model and $a = \sqrt{3}b$ for the Gaussian model
 203 (Goovaerts 1998). Models were fit by the Gauss-Newton nonlinear minimization algorithm in
 204 the R statistical environment (R 2012). The weights N_j/h_j^2 were used in the sum of squares
 205 function.

206 From the set of 5 candidate models, we selected the most parsimonious using Akaike's
 207 Information Criterion corrected for small sample sizes (AIC_c) (Burnham and Anderson 2004),
 208 computed in the R statistical environment (R 2012). We defined the most parsimonious model as
 209 having the lowest AIC_c and where the ΔAIC_c of the next model > 2 (Burnham and Anderson
 210 2002). The most parsimonious model was used to compute the appropriate geostatistical
 211 parameters for each variable.

212

213 RESULTS

214 *Deer use*

215 Stand level deer use during the winter of 2010-11 did not show a consistent trend across
 216 sites relative to the previous 5 winters (Appendix A, Table A1). Pellet group density at Silver
 217 River (610.0 groups ha⁻¹) was similar to previous winters (545.5 ± 99.8 groups ha⁻¹; n = 5). Pellet
 218 group density was greater than any of the previous 5 years at Sylvania (1130.2 groups ha⁻¹ vs.
 219 366.0 ± 105.5 groups ha⁻¹), and lower than the previous 5 years at Ford Forestry Center (107.6
 220 groups ha⁻¹ vs. 355.2 ± 62.8 groups ha⁻¹). We estimated the proportion of each stand that was
 221 directly affected by deer excreta using the observed stand level pellet count densities. We made
 222 the conservative assumptions that 1 excretion event affects a 0.25 m² area (Steinauer and Collins
 223 1995) and that deer urinate and defecate simultaneously (Wallmo 1981). Deer excretion affected
 224 1.5% of the sampled area at Silver River, 2.8% of the Sylvania site, and 0.3% of the Ford
 225 Forestry Center site. Transect fecal pellet group counts followed the same pattern. Pellet group
 226 density was 93 groups ha⁻¹ at Silver River, 280 groups ha⁻¹ at Sylvania, and no pellet groups
 227 were observed at the Ford Forestry Center.

228
 229 *Site level comparisons*

230 Ammonium, nitrate, and total nitrogen ion availability did not differ according to deer
 231 access at the site level based on Monte Carlo randomization tests of the mean (Table 1, Fig. 1).
 232 Direct and total under-canopy radiation did not differ, while diffuse under-canopy radiation was
 233 significantly greater at exclosure sites (observed mean difference, $DIF_{obs} = 0.26 \text{ mol m}^{-2} \text{ day}^{-1}$, p
 234 < 0.001). Herb-layer vegetation attributes did not differ statistically at the site level (Table 1, Fig.
 235 1), although mean cover was more than 50% greater in exclosures. Sapling density was
 236 significantly greater in exclosures ($DIF_{obs} = 1.12 \text{ m}^2$, $p < 0.001$) (see Appendix C, Table C1). A
 237 complete list of species including mean cover by site can be found in Appendix C, Table C2.

238 Monte Carlo randomization tests of the 90th percentile were not significantly different for
 239 ammonium ($DIF_{obs} = 0.31 \text{ mg L}^{-1} \text{ g}^{-1} \text{ resin}$, $p = 0.895$), nitrate ($DIF_{obs} = 0.28 \text{ mg L}^{-1} \text{ g}^{-1} \text{ resin}$, $p =$
 240 1), or total nitrogen ion availability ($DIF_{obs} = 0.49 \text{ mg L}^{-1} \text{ g}^{-1} \text{ resin}$, $p = 0.807$).

241
 242 *Spatial analyses*

243 Complexity of spatial variance structure, as determined by model complexity and type,
 244 differed according to deer access for cover and diversity but not for nitrogen availability or
 245 under-canopy radiation (Table 2). Cover exhibited a nonlinear, exponential spatial variance
 246 structure at deer access and enclosure sites, although the inclusion of a nugget parameter
 247 significantly improved the model in deer enclosures (Table 2). A nugget parameter represents
 248 unexplained variance either due to significant spatial variance at separation distances smaller
 249 than the sampling grain (1 m in our study) or sampling error (Goovaerts 1998). Assuming equal
 250 sampling error at each site, this finding suggests significant spatial variance at very fine (<1 m)
 251 scales in deer enclosures, but not at deer access sites. Spatial variance structure of diversity was
 252 more complex in access sites compared to enclosures (Table 2, Fig. 2). Direct under-canopy
 253 radiation was best represented by nonlinear, Gaussian models with a nugget in deer access and
 254 enclosure sites, with little difference in parameter estimates according to deer access. Other
 255 variables were best represented by 2-parameter exponential models (Table 2). No semivariogram
 256 model estimated a sill > 1 (Table 2), indicating spatial dependence even at the largest separation
 257 distance.

258 Differences in patch size associated with deer access can be examined by comparing the
 259 range of spatial dependence (Table 2, Fig. 2). The patch size of ammonium availability was 66%
 260 smaller in deer access sites compared to deer enclosures (range = 7.47m vs. 3.30m; Table 2, Fig.

261 2). Cover patch size was 64% smaller in deer access sites (range = 16.49m vs. 5.98m; Table 2,
 262 Fig. 2). Nitrate availability and diffuse under-canopy radiation exhibited weaker spatial variance
 263 structure at deer access sites compared to exclosures as evidenced by the selection of simpler,
 264 linear models for access sites (Table 2). The patch size of these variables likely exceeds the
 265 maximum distance of our models because their nugget parameters (y-intercept) are less than 1
 266 and their slopes are small. Diversity patch size in deer exclosures may also exceed the maximum
 267 distance for the same reason. The patch size of direct under-canopy radiation was 26% smaller in
 268 access sites compared to exclosures (Table 2, Fig. 2), which is less of a difference compared to
 269 ammonium and cover.

270 In comparing patch size among variables, cover and diversity were similar to ammonium
 271 availability and direct under-canopy radiation at deer access sites. Within deer exclosures the
 272 patch size of cover was similar to diffuse under-canopy radiation. Direct under-canopy radiation
 273 and nitrate availability patch sizes were similar, and smaller, than ammonium (Table 2, Fig. 2).

274
 275 DISCUSSION

276 Our results support the hypothesis that ungulate excreta maintain more complex spatial
 277 patterns in soil nitrogen resources and herb-layer cover at a spatial extent of 1-20m. Where deer
 278 are present, the spatial pattern of nitrogen availability may be patchier despite a lack of
 279 difference in mean stand level nitrogen availability. Although many studies have documented the
 280 growth-stimulating effects of ungulate excreta, particularly urea-nitrogen (e.g. Steinauer and
 281 Collins 1995, Peek and Forseth 2003), our study demonstrates that it can affect spatial
 282 heterogeneity in resource availability and herb-layer cover at spatial scales relevant to herb-layer
 283 communities of temperate forests.

284 In forest ecosystems light availability is another resource, in addition to nutrient
 285 availability, that limits herb-layer growth (Gilliam and Roberts 2003) and influences the spatial
 286 patterning of herb-layer communities (Scheller and Mladenoff 2002). In our study light seemed
 287 to have a greater influence on the spatial patterning of cover where deer were absent, but not
 288 where they were present. At deer access sites the sapling layer was greatly reduced compared to
 289 exclosures, presumably due to dormant season browsing (Frelich and Lorimer 1985, Rooney et
 290 al. 2000, Witt and Webster 2010). Consequently, the spatial patterning of diffuse under-canopy
 291 radiation was less complex. However, spatial patterning of herb-layer cover and diversity
 292 exhibited smaller patch sizes despite less complex spatial patterning in diffuse radiation. In deer
 293 exclosures the sapling layer and spatial pattern of diffuse radiation were more complex, and the
 294 patch size of cover closely resembled that of diffuse radiation. Deer have been known to
 295 homogenize plant communities across spatial gradients of resource availability via browsing
 296 (e.g. Holmes and Webster 2011), but in our study deer appear to have increased heterogeneity in
 297 understory cover.

298 Although deer and other ungulates are generally regarded as homogenizers of plant
 299 communities (e.g. Rooney et al. 2004, Webster et al. 2005, Rooney 2009), deer effects on
 300 vegetation operate within a broader ecological context (Schmitz and Sinclair 1997). Until
 301 recently studies of deer impacts were limited to case studies where a problem was perceived *a*
 302 *priori*, making them susceptible to pseudoreplication (Côté et al. 2004). Several recent studies
 303 have highlighted the broader ecological function of deer in forest ecosystems. For example,
 304 Royo et al. (2010) found that at intermediate deer densities browsing interacts with other
 305 disturbances, such as fire and gap creation, to increase plant diversity. Deer exclusion reduced
 306 diversity by allowing fast-growing, palatable plant species to dominate the community following

307 disturbance. Long-term exclusion of browsing ungulates can lead to a similar outcome even in
 308 the absence of disturbance (Perrin et al. 2011). Deer abundance is often thought of as an
 309 indicator of deer impacts, however, deer impacts also depend on the abundance of palatable
 310 plants (Schmitz and Sinclair 1997) and landscape context (Rutherford and Schmitz 2010, Hurley
 311 et al. 2012). At the landscape scale deer may function as vectors for nutrient transport from
 312 ecosystems of greater nutrient availability to those of lower nutrient availability (Seagle 2003,
 313 Bump et al. 2009a, Abbas et al. 2012). At finer scales ungulate carcasses can create nutrient
 314 hotspots that affect forest and prairie plant community composition (Towne 2000, Bump et al.
 315 2009b).

316 Our results likely apply to other deer populations and ungulate species because of
 317 seasonally (or diurnally) dynamic aggregations, dispersals, and migrations common to these
 318 species. Consequently, our study highlights the importance of seasonal timing in both resource
 319 inputs and herbivory to the outcome of complex feedbacks between herbivores and the spatial
 320 distribution of resources. A plant's ability to compensate for herbivory depends on the timing of
 321 herbivory and nutrient availability, in addition to competition with other plants (Maschinski and
 322 Whitham 1989). Hemlock forests are used by deer primarily for winter cover rather than food.
 323 Deer migrate from hemlock stands to more productive habitats as severe winter weather subsides
 324 (Verme 1973), so that most deer herbivory occurs during the dormant season (Frelich and
 325 Lorimer 1985, Rooney et al. 2000, Witt and Webster 2010). Due to seasonal deer use, much of
 326 the deer-source nitrogen inputs occur during winter and enter the soil pool as a pulse during
 327 spring snowmelt. Spring ephemerals and soil microorganisms would benefit directly from these
 328 nitrogen pulses, and capture nitrogen for later uptake by summer vegetation (Zak et al. 1990).
 329 Plant community heterogeneity has previously been linked to deer use in remnant hemlock

330 stands (Jensen et al. 2011). Therefore, we hypothesize that the seasonal decoupling of ungulate
 331 habitat use and plant growth has allowed understory plants the opportunity to respond to
 332 ungulate-excreted nitrogen additions without greater risk of being consumed by ungulates. The
 333 patchy spatial distribution of deer excreta results in patches of increased vegetation growth,
 334 increasing the spatial heterogeneity of vegetation cover.

335 The impact of deer on neighborhood scale heterogeneity in nitrogen availability and herb-
 336 layer cover suggests a link between fine scale and landscape scale processes. Ungulates select
 337 habitat patches at coarse landscape-level scales, whereas impacts on vegetation occur at the scale
 338 of individual plants (Weisberg et al. 2006). Consequently, landscape configuration can modulate
 339 the impact of ungulate herbivory on vegetation at a given ungulate density (Hurley et al. 2012).
 340 In the northern hardwood-hemlock forest mosaic of our study, deer selection of conifer-
 341 dominated winter habitat is influenced by landscape context in addition to stand level variables
 342 (Witt et al. 2012). In our study seasonal patterns in deer habitat selection reduced cover of large
 343 seedlings and saplings that grow above the snowpack. Growing season herbivory may be
 344 reducing cover in access sites relative to exclosures, although the reduction was not statistically
 345 significant. Moderate levels of growing season herbivory may result in greater diversity even if
 346 cover is reduced (Royo et al. 2010). If moderate growing season herbivory reduces total cover,
 347 deer may still increase heterogeneity through patchy nitrogenous waste deposition (Steinauer and
 348 Collins 1995, Augustine and Frank 2001), trampling (Heckel et al. 2010), and selective
 349 herbivory (Augustine and McNaughton 1998). Similarly, the patch size of nitrogen and cover
 350 may vary over the landscape with changes in deer use, linking fine scale and coarse scale
 351 processes. This question could be explored further by incorporating deer access sites across a
 352 gradient of deer densities.

353 Our failure to detect nitrogen hotspots at deer access sites does not compromise our
 354 conclusion that ungulate excreta increase spatial heterogeneity in nitrogen availability. First,
 355 most of the deer-excreted nitrogen measured by ion-exchange resin bags was deposited during
 356 winter and passed through the snowpack before reaching the soil. This process is likely to have
 357 increased the area affected by an excretion event while making its patch boundary more diffuse
 358 and difficult to detect. Second, resin bags were buried for several weeks after snowmelt. Other
 359 nitrogen inputs during this time may have masked deer-excreted nitrogen. We retrieved resin
 360 bags during the vegetation survey to ensure that we measured the nitrogen available to the
 361 observed vegetation community. Third, it is highly unlikely that we placed a resin bag in the
 362 exact location that a deer urinated or defecated during winter 2010-11 given that fecal pellets
 363 occurred in < 3% of the sampled area. The observed differences in spatial patterns may be the
 364 cumulative result of deer-excreted nitrogen inputs over multiple seasons.

365 Browsing ungulates may be an important source of spatial heterogeneity in forest
 366 ecosystems. Human activities are greatly altering nitrogen cycling in many temperate forest
 367 ecosystems, and one outcome is the homogenization of nitrogen availability (Gilliam 2006).
 368 Atmospheric nitrogen deposition levels are less elevated in the northern Great Lakes region
 369 where our study took place compared to more industrialized areas (e.g. Gilliam 2006, 2007),
 370 although they are greater than annual nitrogen sequestration by plants (Talhelm et al. 2012).
 371 Herb-layer communities contain much of the biodiversity in temperate forests (Gilliam 2007),
 372 but biodiversity declines as a result of nitrogen saturation and homogenization (Gilliam 2006).
 373 Therefore, ecological processes that increase spatial heterogeneity of nitrogen availability and
 374 are scale-dependent are important to maintaining biodiversity. Ungulates may increase or
 375 decrease heterogeneity of these processes depending on ecological context, and may be an

376 important component of unaltered forest nitrogen cycles as they are in grasslands (e.g.
 377 McNaughton 1985, Augustine et al. 2003). Although ungulate exclosures are useful for restoring
 378 vegetation in many cases, they may not be effective at restoring spatial patterns of resource
 379 availability.

380 Our results demonstrate that forest ungulates can create complex spatial patterns in soil
 381 nitrogen, a critical and limiting terrestrial resource. The ecological importance of this effect is
 382 contingent upon the scale of inference and the seasonal timing of ungulate impacts relative to
 383 ecosystem response. Ungulates are common in forest ecosystems, and may be an important
 384 ecological link between fine scale and landscape scale processes that are further modulated by
 385 seasonally dynamic habitat selection. Our main results highlight the general need to examine
 386 (and re-examine) the dynamic role of ungulate species in affecting ecosystem processes.
 387 Questions of scale and heterogeneity are prominent in ecology because they provide a link
 388 between ecosystem and animal ecology that advances conservation science (Levin 1992, Ritchie
 389 2010, Loreau 2010). Forest ungulate ecology may be better understood when viewed within a
 390 broad ecological context that includes scale, heterogeneity, and ecosystem processes.

391

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558

559 SUPPLEMENTAL MATERIAL

560 **Appendix A**

561 Ottawa National Forest and Ford Forestry Center study site information.

562 **Appendix B**

563 Detailed description of deer use survey, ion-exchange resin bag, and spatial variance modeling
564 methodologies.

565 **Appendix C**

566 Data tables describing understory tree height class distributions and mean cover of herb-layer
567 species by site.

568

569 TABLES

570 TABLE 1. Comparison of stand level means by Monte Carlo randomization tests.

Variable	Access – mean (SE)	Exclosure – mean (SE)	DIF_{obs}^e	p^f
Ammonium	2.71 (0.36)	2.70 (0.40)	0.01	1.000
Nitrate	1.37 (0.46)	1.09 (0.35)	0.29	0.517
Total N ion ^a	4.09 (0.63)	3.79 (0.30)	0.30	0.682
Direct UCR ^b	5.58 (0.49)	7.28 (0.39)	1.69	0.107
Diffuse UCR	0.80 (0.10)	1.06 (0.08)	0.26	<0.001
Total UCR ^c	6.39 (0.54)	8.34 (0.43)	1.95	0.094
Herb cover ^d	15.4 (3.9)	36.0 (4.7)	20.6	0.097
<i>S</i>	4.26 (0.53)	5.97 (0.98)	1.71	0.084
<i>H'</i>	0.93 (0.091)	1.26 (0.15)	0.33	0.104
<i>E</i>	0.72 (0.03)	0.75 (0.01)	0.03	0.373
Seedling density	3.95 (1.40)	6.42 (1.81)	2.47	0.377
Sapling density	0.01 (0.01)	1.13 (0.57)	1.12	<0.001

571 ^a Total N ion = sum of ammonium concentration and nitrate concentration

572 ^b under-canopy radiation

573 ^c Total UCR = sum of direct UCR and diffuse UCR

574 ^d percent cover of herb-layer vegetation

575 ^e observed difference = $|\text{mean}_{\text{access}} - \text{mean}_{\text{exclosure}}|$

576 ^f $p = \text{proportion of } DIF_{sim} \geq DIF_{obs}$, where DIF_{sim} are from a randomized distribution

577 TABLE 2. Parameter estimates for the most parsimonious (based on ΔAIC_c) semivariogram models.

Variable	Access						Exclosure					
	Model	Range ^d (m)	Sill ^f (γ)	Nug. ^g (γ)	<i>RSE</i> ^h	<i>df</i>	Model	Range (m)	Sill (γ)	Nug. (γ)	<i>RSE</i>	<i>df</i>
Ammonium	Exponential	3.30	0.91	NA	0.363	24	Exponential	7.47	0.86	NA	0.115	24
Nitrate	Linear ^b	NA ^c	NA	0.81	0.136	24	Exponential	2.80	0.66	NA	0.144	24
Direct UCR ^a	Gaussian	2.57	0.84	0.18	0.092	23	Gaussian	3.45	0.94	0.10	0.158	23
Diffuse UCR	Linear ^c	NA	NA	0.15	0.051	24	Exponential	18.84	0.69	NA	0.100	24
Herb cover	Exponential	5.98	0.89	NA	0.123	24	Exponential	16.49	0.57	0.09	0.063	23
Herb diversity	Exponential	5.70	0.87	NA	0.124	24	White noise	NA	NA	0.51	0.149	25

578 ^a UCR under-canopy (solar) radiation

579 ^b Slope parameter $m = -0.01$

580 ^c Slope parameter $m = 0.01$

581 ^d Range = $3b$ for exponential models; range = $\sqrt{3b}$ for Gaussian models

582 ^e NA Not applicable to selected model

583 ^f Sill = $C + \epsilon$

584 ^g Nugget = ϵ for spherical, exponential, and Gaussian models; nugget = mean ($\epsilon(h)$) for white noise and linear models

585 ^h *RSE* residual standard error

586

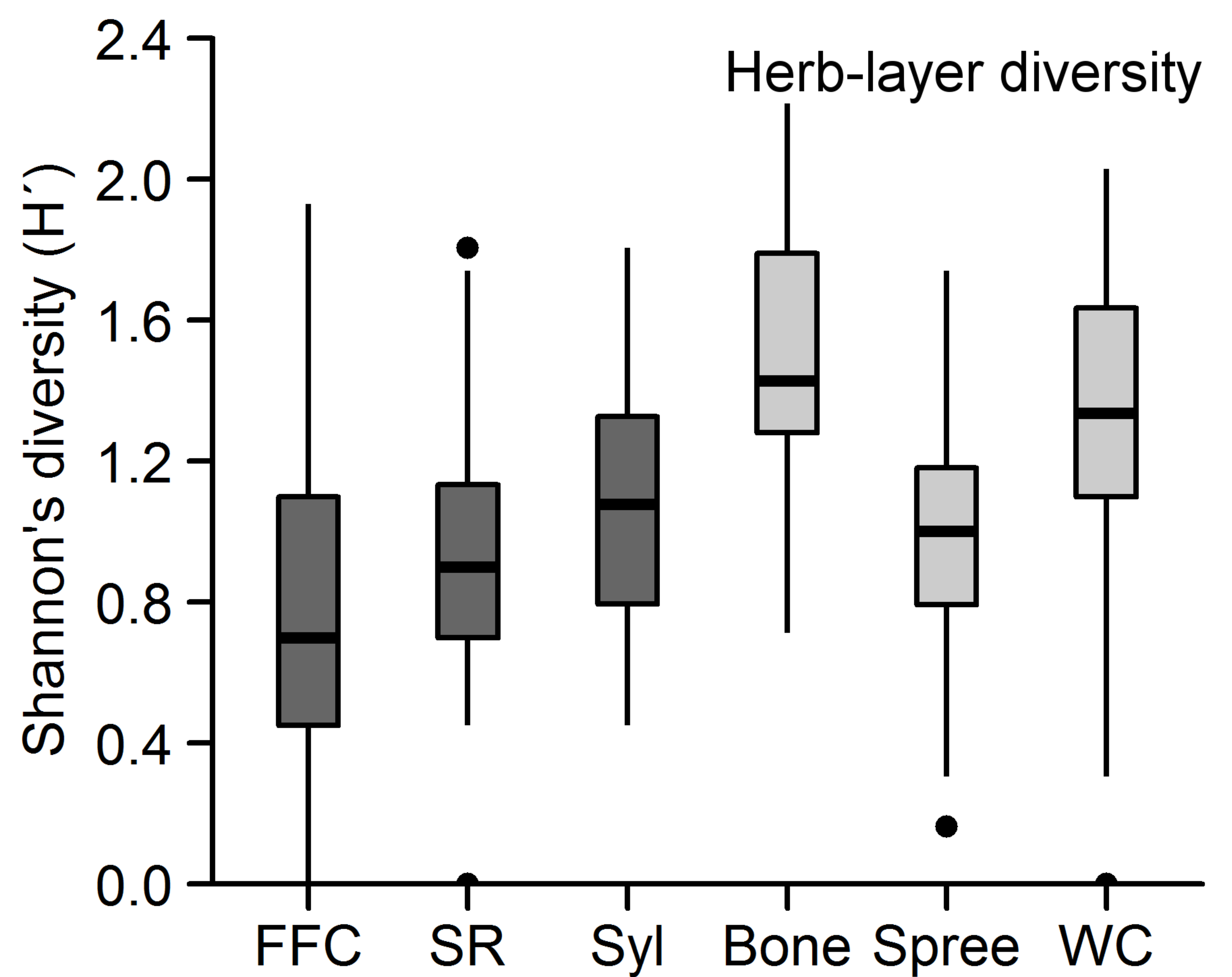
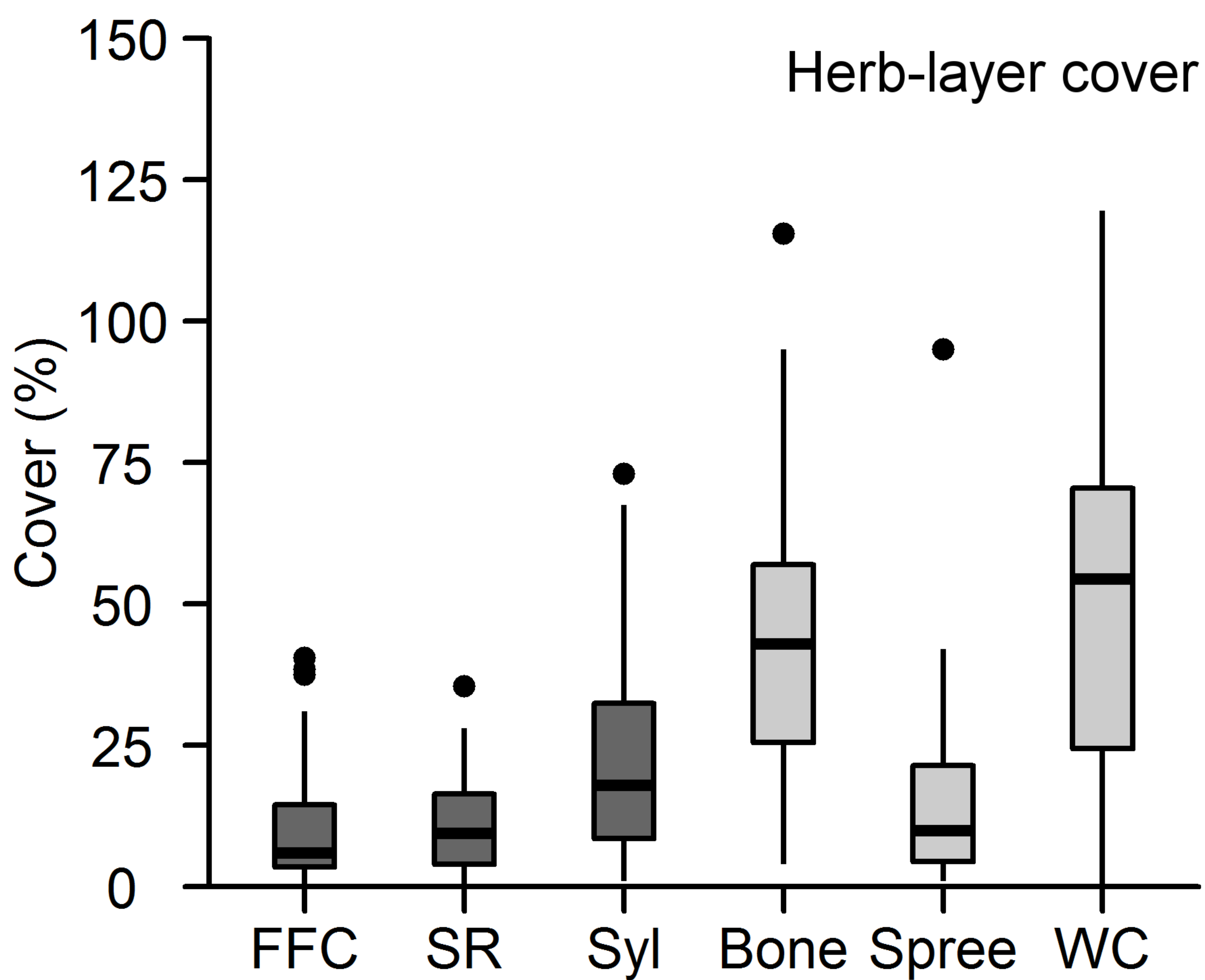
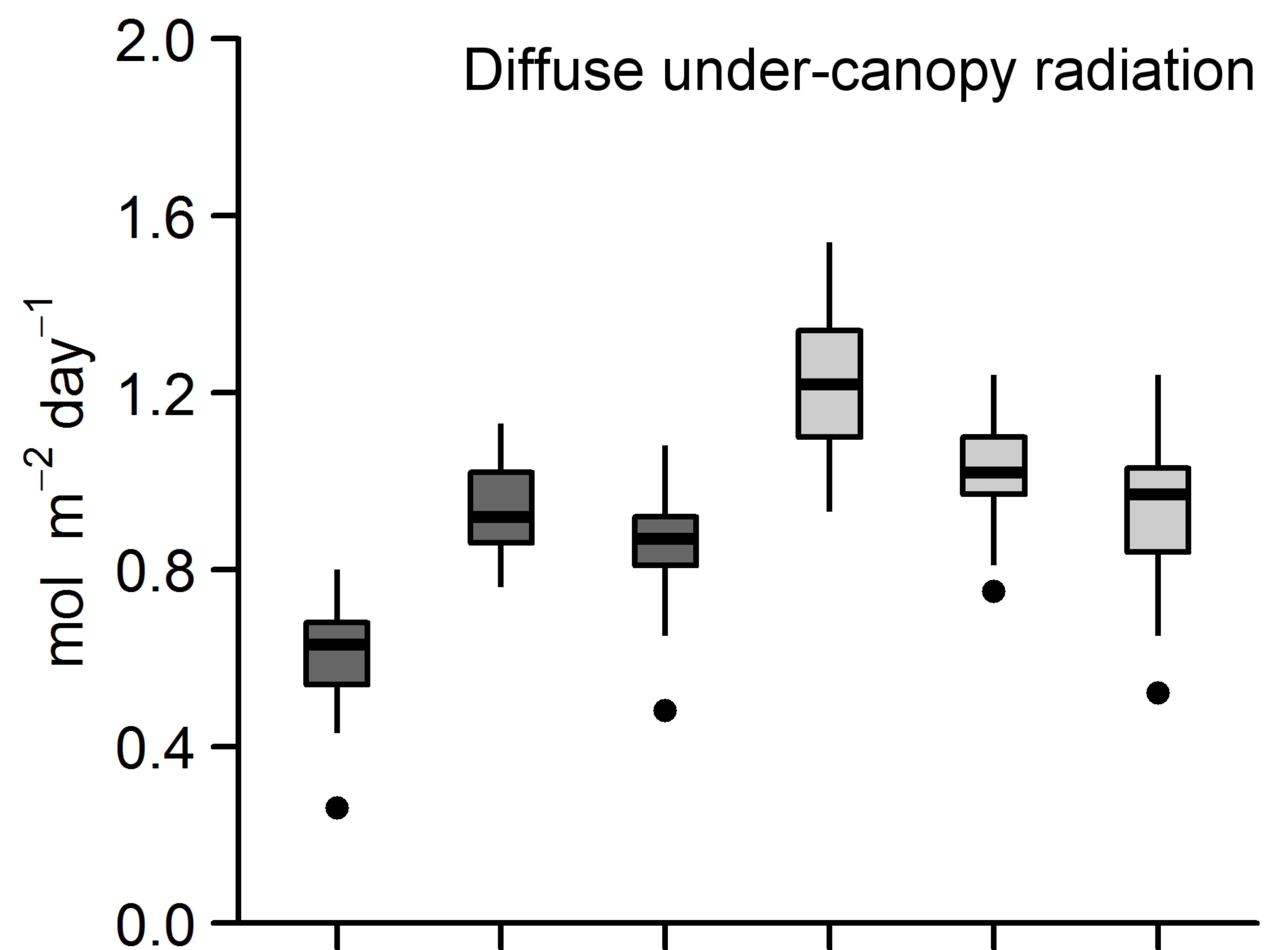
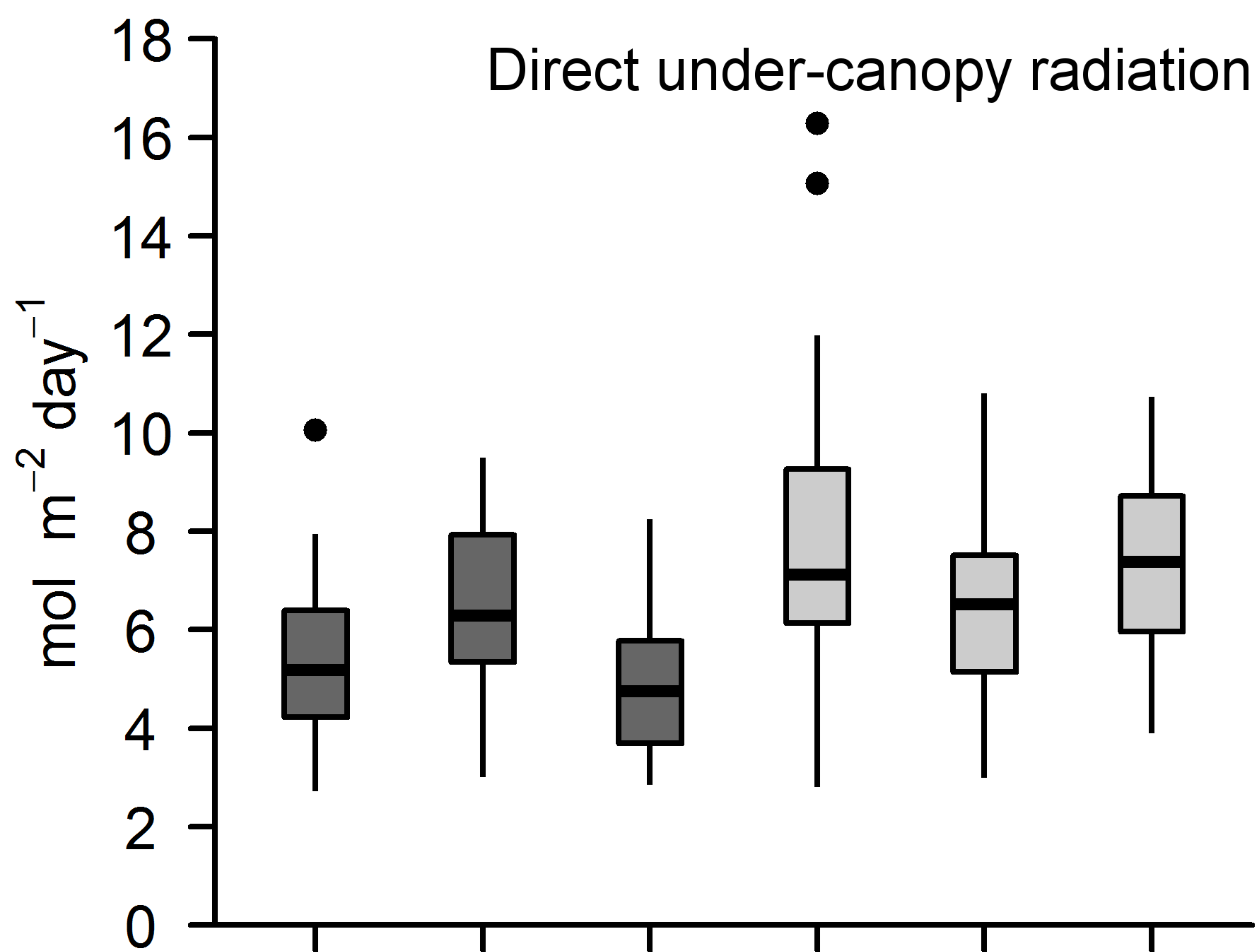
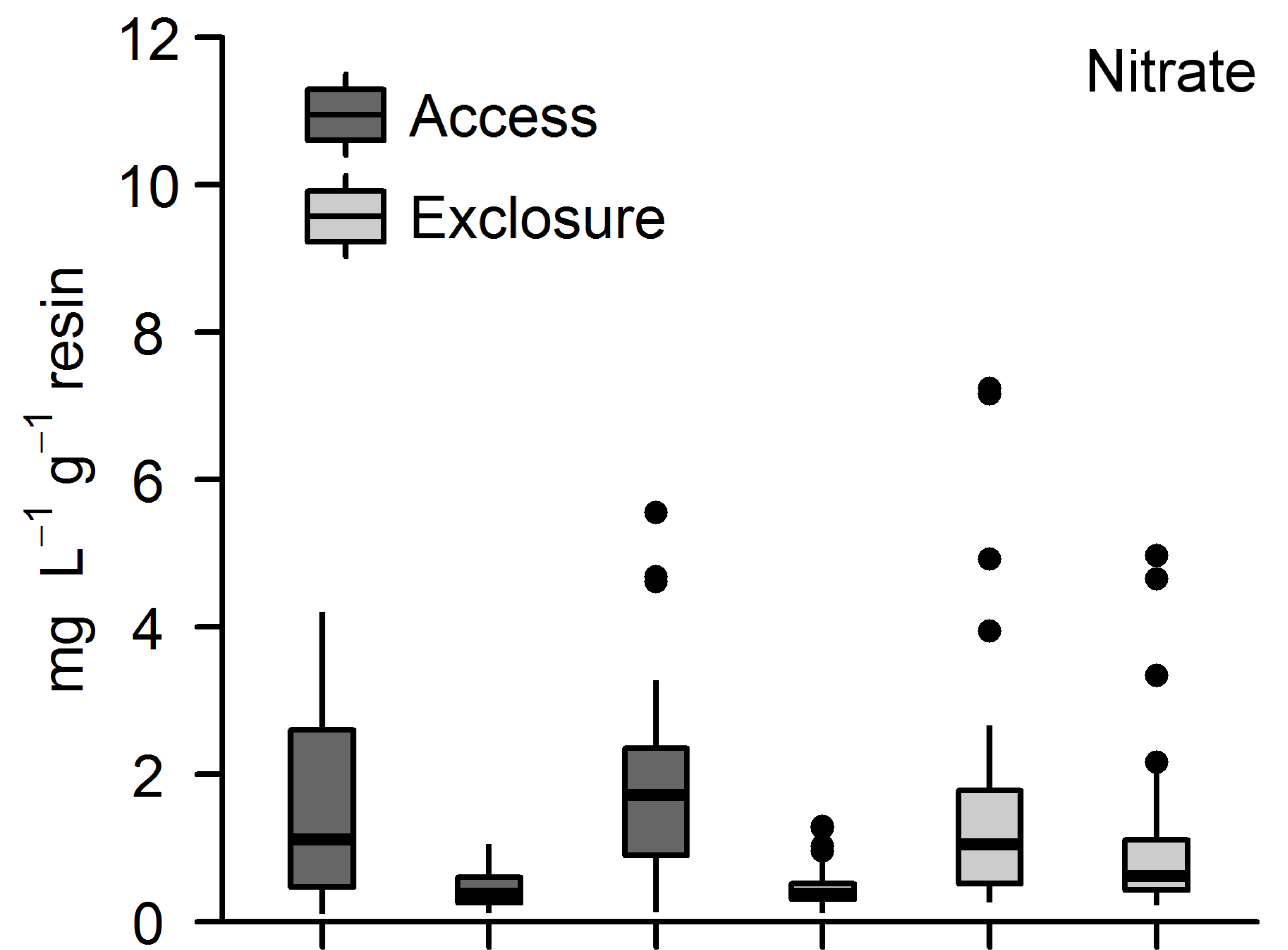
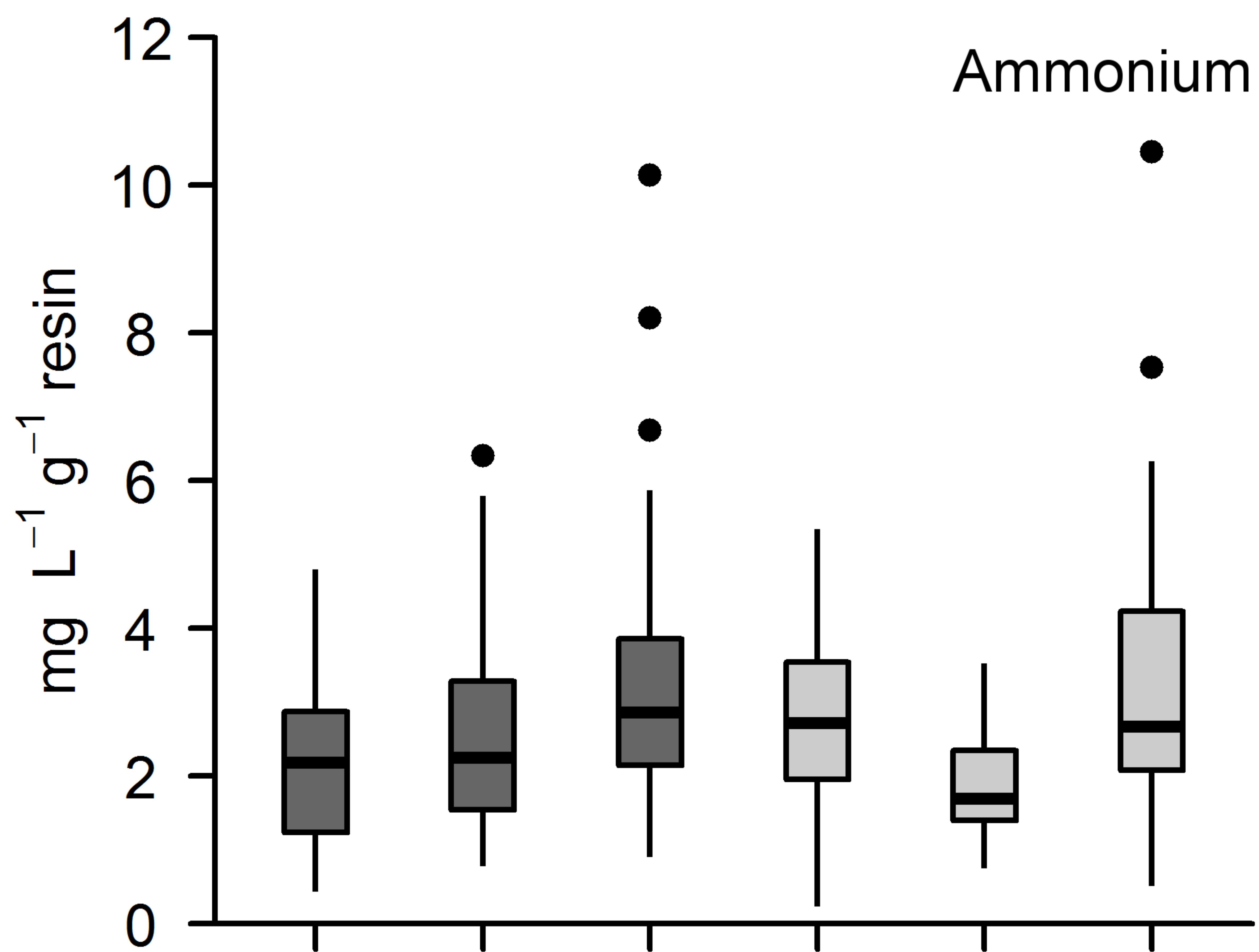
587 FIGURE LEGENDS

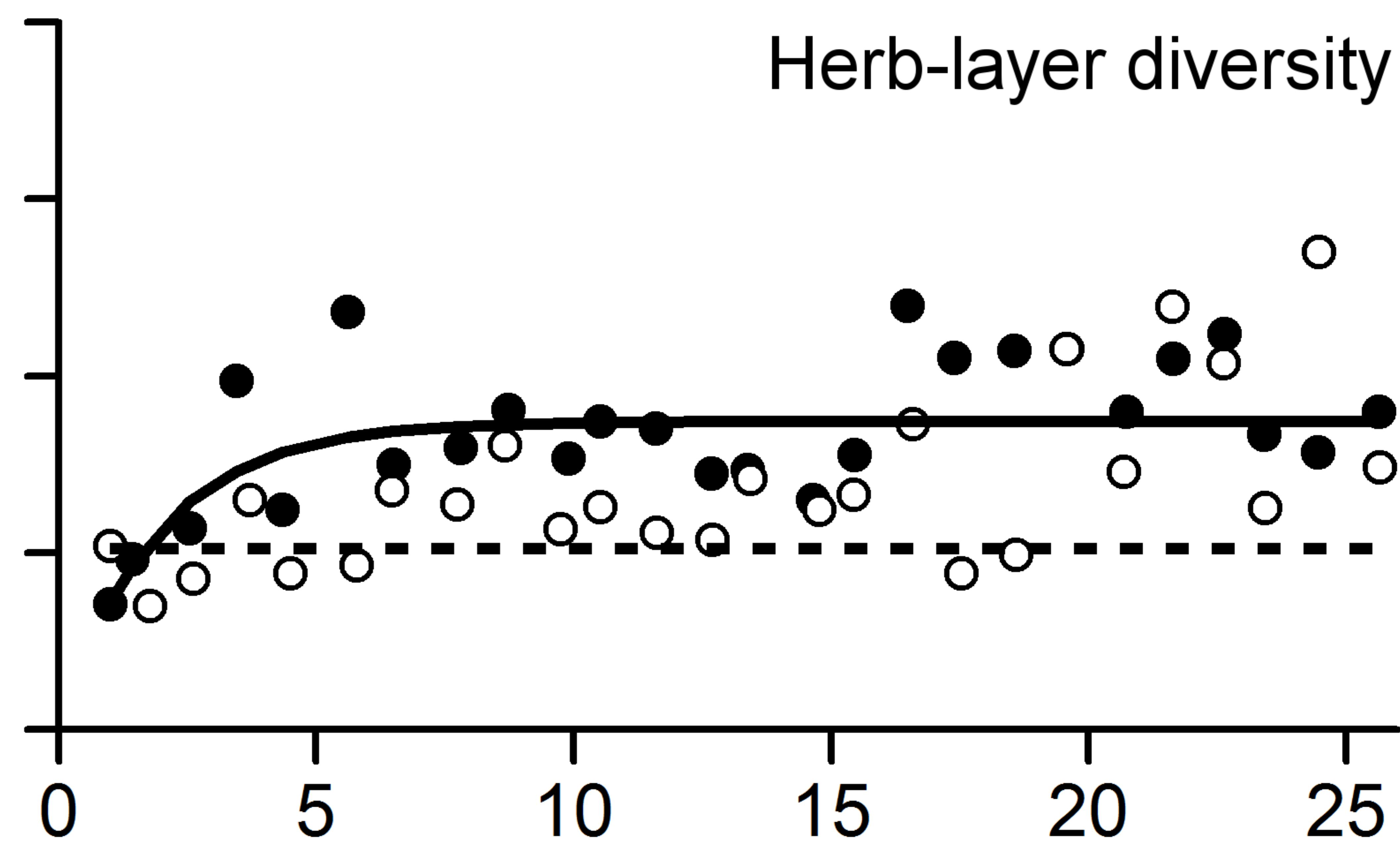
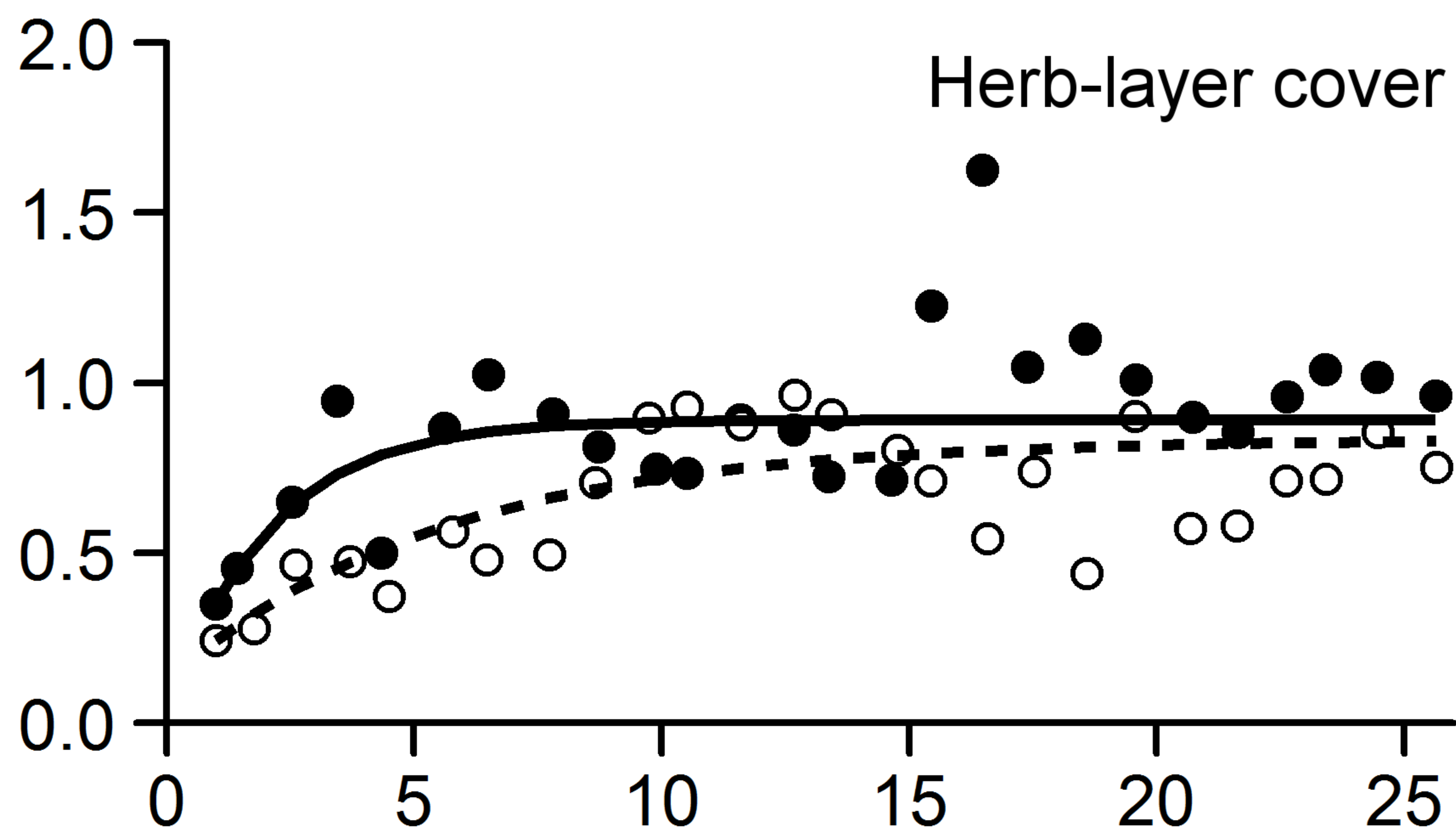
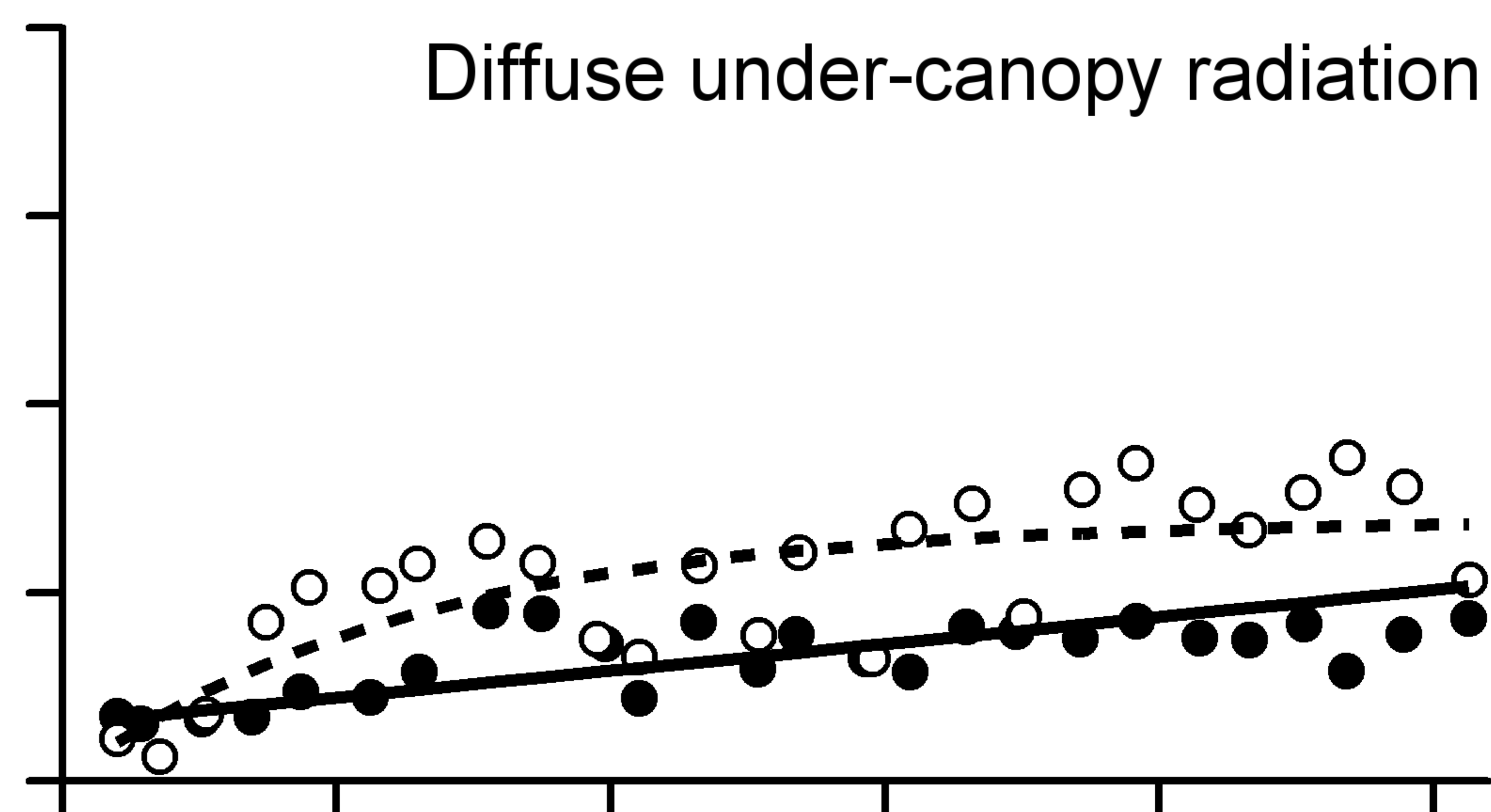
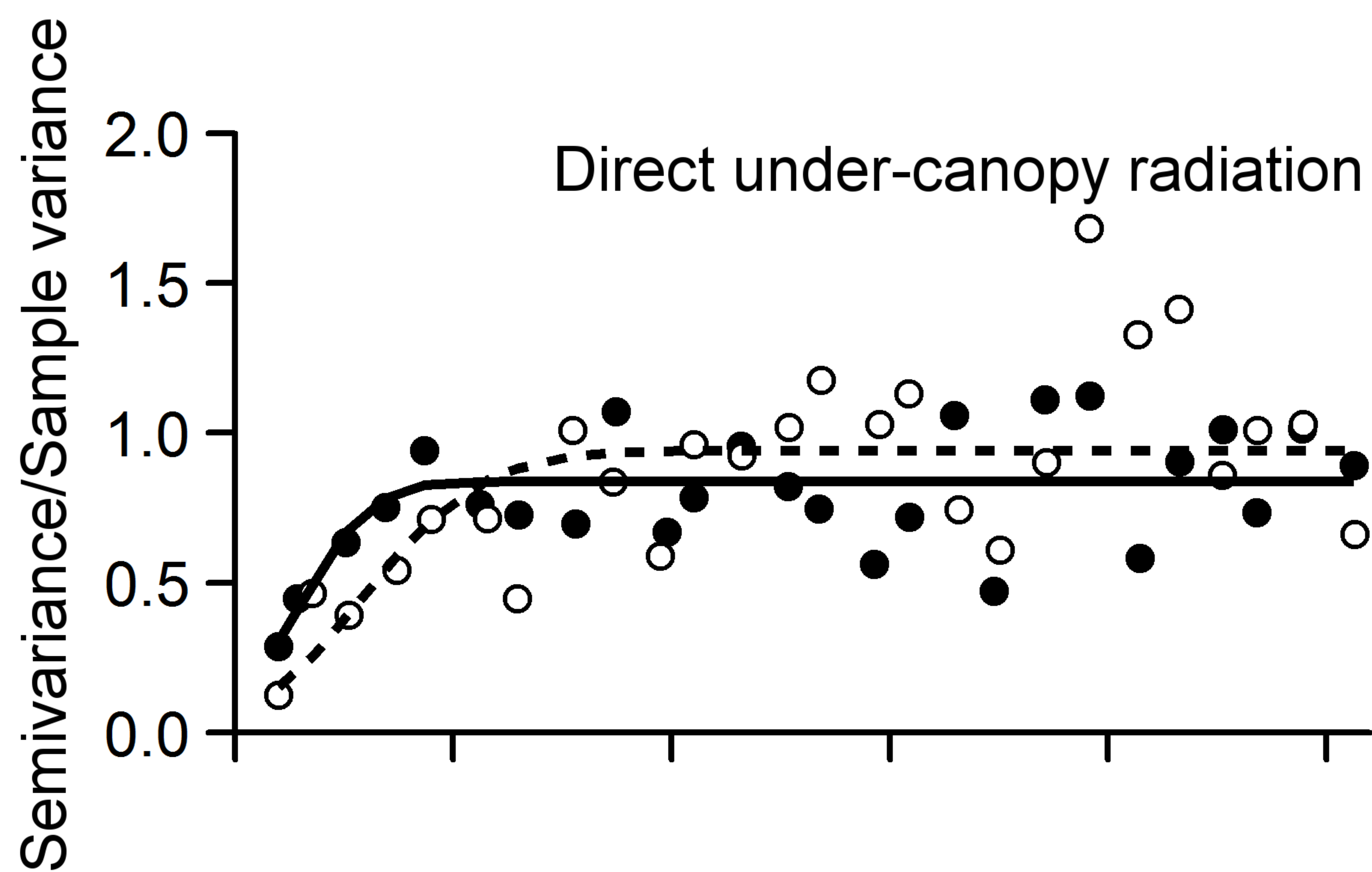
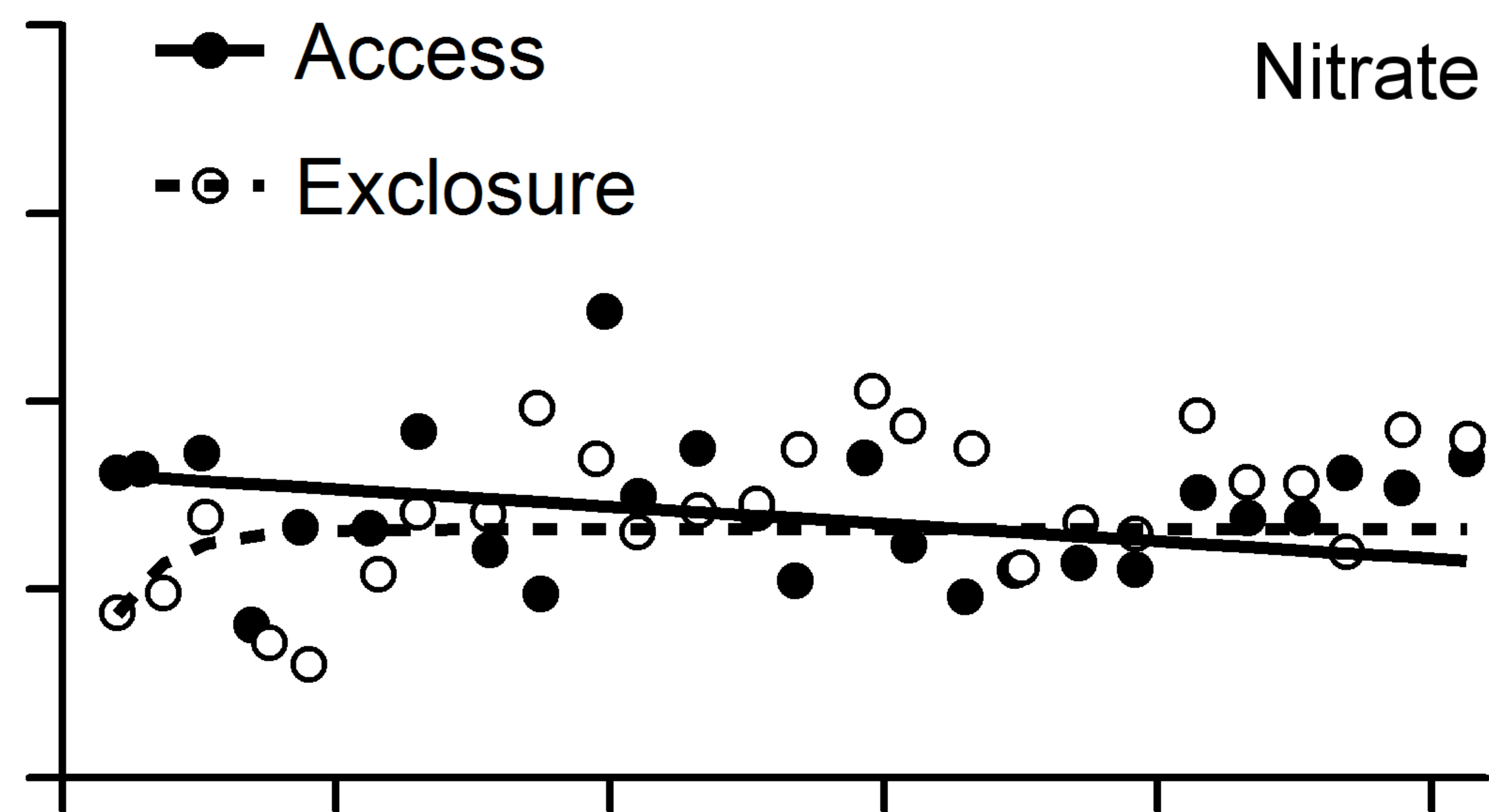
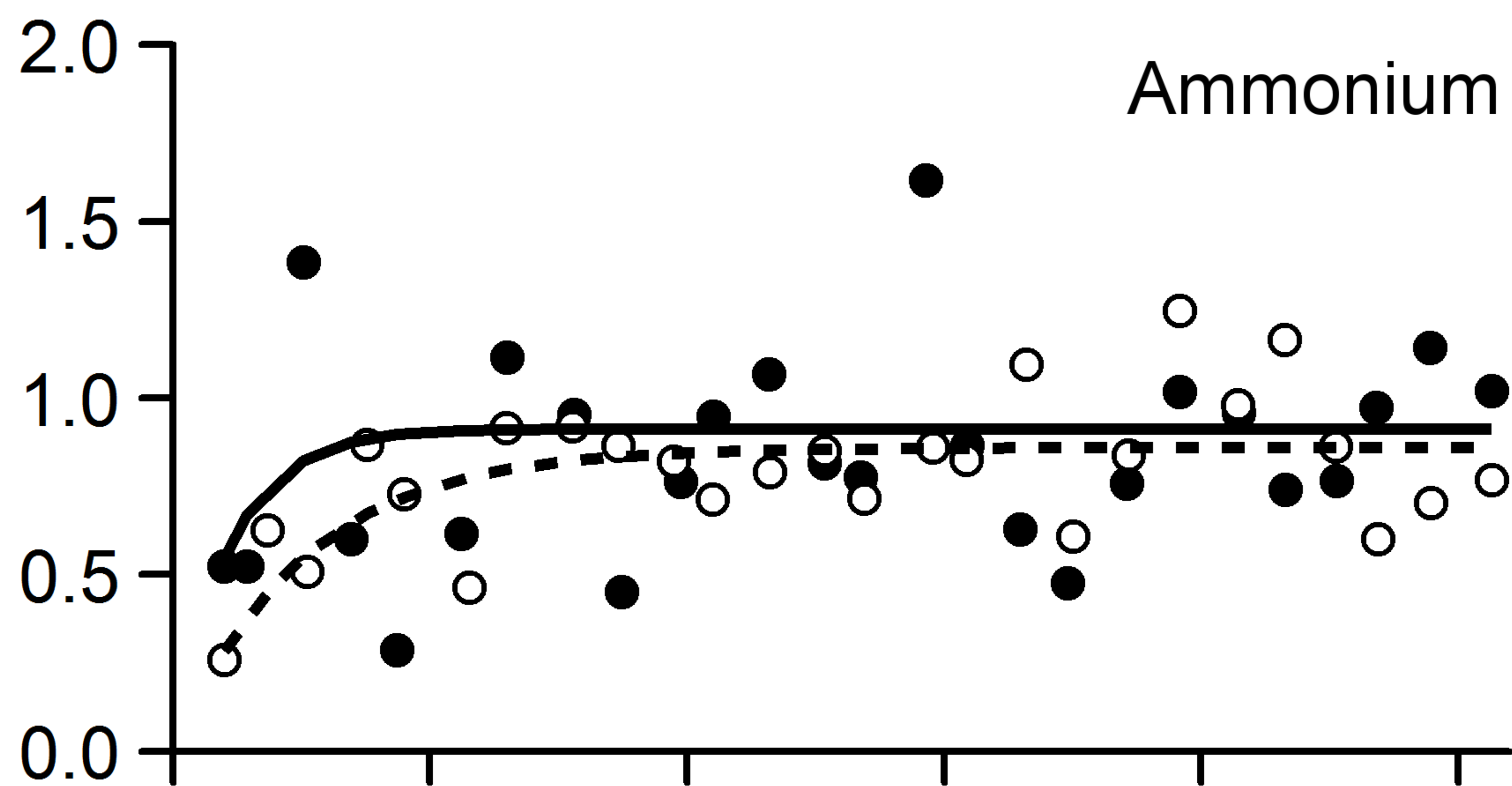
588 FIG. 1. Boxplots of each variable by site. In each box, the dark middle line represents the median,
 589 and the upper and lower extents of the box represent the 75th and 25th percentiles, respectively.
 590 Lines extend to 1.5 times the interquartile range (difference of 75th and 25th percentiles). Black
 591 circles indicate outliers. Site name abbreviations: “FFC” = Ford Forestry Center, “SR” = Silver
 592 River, “Syl” = Sylvania, “Bone” = Boneyard, “Spree” = Spree, “WC” = Walton Creek.

593

594 FIG. 2. Empirical semivariograms (circles) and modeled semivariograms (lines), grouped
 595 according to deer access. See Table 2 for model identification and parameter estimates.

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Distance (m)